THE COMPARATIVE MORPHOLOGY OF THE MOUTHPARTS OF THE ORDER COLEOP-TERA TREATED FROM THE STAND-POINT OF PHYLOGENY¹

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INTRODUCTION

With the exception of Stickney's monograph on the head capsule, Tanner's paper on the female genitalia, and Forbes' work on the wings, very little has been done on the comparative morphology of adult Coleoptera. Only a few scattered papers deal with the mouthparts of different species or with a single family at the most. The present studies of the labia and maxillæ of the representatives of most of the coleopterous families have been made with the purpose of supplementing Stickney's extensive and thorough work of the head capsules. It is hoped that these studies may add to the knowledge of the phylogenetic groupings of the families within the order.

The arrangement of the families in Leng's "Catalogue of Coleoptera of America north of Mexico" has been followed. A representative of each family has been chosen, more or less at random, for study. The consideration of members of the various subfamilies would undoubtedly have made comparisons much more complete, but due to the fact that suitable material was not available, the subfamilies have not been included. The Eucinetidæ, Nosodendridæ, Trogidae, and Byturidæ, which are treated by Leng (1920) as subfamilies, have not been considered in this paper. The Telegeusidæ, Micromalthidæ, Eurystethidæ, Plastoceridæ, Monoedidæ, and Brathinidæ have been omitted because they were either unobtainable or too minute to study with the equipment available.

As Stickney (1923) indicates in the case of the head capsule, attempts to arrange the figures of the labium and maxilla in a series from the generalized to the more specialized types proved unsuccessful. Primitive features of some structures are in many

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cases combined with specialized features of other structures. For this reason, the figures of the one-hundred families involved in this paper have been arranged as nearly as possible in the family groupings presented by Leng in the "Catalogue of the Coleoptera."

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COLEOPTERA

SUBORDER ADEPHAGA

CARABOIDEA

- 1. Cicindelidæ—*Cicindela sexguttata* Fab. (Fig. 1)
- 2. Carabidæ—Harpalus caliginosus (Fab.) (Fig. 2)
- 3. Amphizoidæ—Amphizoa isolens Lec. (Fig. 6)
- 4. Omophronidæ—Omophron americanum Dej. (Fig. 3)
- 5. Haliplidæ—Laccophilus maculosus (Germ.) (Fig. 4)
- 6. Dytiscidæ—Colymbetes sculptilis Harr. (Fig. 5)

GYRINOIDEA

7. Gyrinidæ—Dineutes vittatus (Germ.) (Fig. 7)

8. Paussidæ—Paussus hova (Fig. 8)

SUBORDER POLYPHAGA

HYDROPHILOIDEA

9. Hydrophilidæ—Tropisternus glaber (Hbst.) (Fig. 9)

SILPHOIDEA

10. Platypsyllidæ—*Platypsyllus castoris* Rits. (Fig. 10)

11. Leptinidæ—Leptinus testaceus Müll. (Fig. 11)

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- 12. Silphidæ—Silpha americana L. (Fig. 13)
- 13. Clambidæ—Clambus punctulum Beck. (Fig. 12)
- 14. Scydmaenidæ-Euconnus similis Blatch. (Fig. 14)
- 15. Orthoperidæ—Orthoperus brunnipes Gyll. (Fig. 15)

STAPHYLINOIDEA

- 16. Staphylinidæ—Staphylinus vulpinus Nordm. (Fig. 16)
- 17. Pselaphidæ—Pselaphus dresdensis Hbst. (Fig. 17)
- 18. Clavigeridæ—Claviger testaceus (Fig. 19)
- 19. Ptilidæ—Trichopteryx lata Motsch. (Fig. 18)
- 20. Sphaeriidæ—Sphaerius acaroides Waltl. (Fig. 20)
- 21. Scaphidiidæ—Scaphidium quadrimaculatum Oliv. (Fig. 21)
- 22. Sphaeritidæ—Sphaerites glabratus (Fab.) (Fig. 22)
- 23. Histeridæ—Hister obtusatus Harr. (Fig. 23)

CANTHAROIDEA

- 24. Lycidæ—Eros aurora Hbst. (Fig. 24)
- 25. Lampyridæ—Lucidota atra (Fab.) (Fig. 25)
- 26. Phengodidæ-Phengodes sp. (Fig. 26)
- 27. Cantharidæ—Cantharis andersoni Frost (Fig. 27)
- 28. Melyridæ—Malachius aeneus (L.) (Fig. 28)
- 29. Cleridæ—Trichodes ornatus Say (Fig. 29)
- 30. Corynetidæ—Chariessa pilosa Forst. (Fig. 30)

LYMEXYLOIDEA

31. Lymexylidæ—Hylocoetus dermestoides L. (Fig. 32)

CUPEDOIDEA

32. Cupedidæ—*Cupes latreillei* Sol. (Fig. 33)

Mordelloidea

- 33. Cephaloidæ—Cephaloon lepturides Newm. (Fig. 34)
- 34. Oedemeridæ—Ditylus laevis Fabr. (Fig. 35)
- 35. Mordellidæ—Tomoxia bidentata (Say) (Fig. 36)
- 36. Rhipiphoridæ—Rhipiphorus dimidiatus Fabr. (Fig. 37)
- 37. Meloidæ—Nemognatha piezata Fab. (Fig. 38)
- 38. Othniidæ—Othnius kraatzi (Fig. 31)
- 39. Pythidæ—Pytho americanus Kyb. (Fig. 39)

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- 40. Pyrochroidæ—Pyrochroa coccinea L. (Fig. 40)
- 41. Pedilidæ—Pedilus collaris (Say) (Fig. 41)
- 42. Anthicidæ—Notoxus calcaratus Horn (Fig. 42)
- 43. Euglenidæ—Euglenes pruinosus (Fig. 43)

ELATEROIDEA

- 44. Cerophytidæ—Cerophytum elateroides Latr. (Fig. 44)
- 45. Cebrionidæ—Cebrio gigas Fabr. (Fig. 45)
- 46. Rhipiceridæ-Sandalus segnis (Fig. 46)
- 47. Elateridæ—Alaus oculatus (L.) (Fig. 47)
- 48. Melasidæ—Eucnemis capucina Ahrens. (Fig. 48)
- 49. Throscidæ—Throscus dermestoides L. (Fig. 49)
- 50. Buprestidæ—Buprestis fasciata Fab. (Fig. 50)

DRYOPOIDEA

- 51. Psephinidæ—Psephenus lecontei (Lec.) (Fig. 51)
- 52. Dryopidæ-Potamophilus acuminatus Fabr. (Fig. 52)
- 53. Helmidæ-Helmis mangei (Fig. 53)
- 54. Heteroceridæ—Heterocerus parallelus Kyrnick (Fig. 55)
- 55. Georyssidæ—Georyssus lavicollis Germ. (Fig. 54)

DASCILLOIDEA

- 56. Dascillidæ—Dascillus cervinus L. (Fig. 56.)
- 57. Helodidæ—Scrites tibialis Guer. (Fig. 57)

BYRRHOIDEA

- 58. Chelonariidæ—Chelonarium ornatum Klug (Fig. 58)
- 59. Dermestidæ—Dermestes lardarius L. (Fig. 59)
- 60. Byrrhidæ—Byrrhus americanus Lec. (Fig. 60)

RHYSODOIDEA

61. Rhysodidæ—Rhysodes sulcatus Fabr. (Fig. 61)

CUCUJOIDEA

- 62. Ostomidæ—Ostoma grossa (L.) (Fig. 62)
- 63. Nitidulidæ—Prometobia sexmaculata (Say) (Fig. 63)
- 64. Rhizophagidæ—Rhizophagus picipes (Fig. 64)
- 65. Monotomidæ—Monotoma conicicollis (Fig. 65)
- 66. Cucujidæ—Cucujus clavipes Fab. (Fig. 66)

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- 67. Erotylidæ-Mega lodacne grandipennis (Fig. 67)
- 68. Derodontidæ—Derodontus maculatus (Melsh.) · (Fig. 68)
- Cryptophagidæ—Antherophagus ochraceus Melsh. (Fig. 69)
- 70. Mycetophagidæ—Mycetophagus punctatus Say (Fig. 70)
- 71. Colydiidæ—Trachypholis ornatus (Fig. 71)
- 72. Murmidiidæ—Murmidius ovalis Beck. (Fig. 72)
- 73. Lathridiidæ—Lathridius lardarius De G. (Fig. 73)
- 74. Mycetæidæ—Mycetæa hirta (Marsh.) (Fig. 74)
- 75. Endomychidæ—Lycoperdina ferruginea Lec. (Fig. 75)
- 76. Phalacridæ—Phalacrus grossus Erichs. (Fig. 76)
- 77. Coccinellidæ—Anatis quindecimpunctata (Oliv.) (Fig. 77)

TENEBRIONOIDEA

- 78. Alleculidæ-Hymenorus melsheimeri Csy. (Fig. 78)
- 79. Tenebrionidæ—Alobates pennsylvanica (De G.) (Fig. 80)
- 80. Lagriidæ—Arthromacra anea (Say) (Fig. 79)
- 81. Monommidæ—Monomma maximum (Fig. 81)
- 82. Melandryidæ—Penthe obliquata (Fab.) (Fig. 82)

BOSTRICHOIDEA

- 83. Ptinidæ—Oligomerus brunneus Oliv. (Fig. 83)
- 84. Anobiidæ—Sitodrepa panicea (L.) (Fig. 84)
- 85. Bostrichidæ—Apate terebrans Pall. (Fig. 85)
- 86. Lyctidæ—Lyctus linearis (Gœze) (Fig. 86)
- 87. Sphindidæ-Sphindus dubius Gyllh. (Fig. 87)
- 88. Cisidæ—*Cis boleti* Scopoli (Fig. 88)

SCARABAEOIDEA

- 89. Scarabæidæ—Geotrupes splendidus (Fab.) (Fig. 89)
- 90. Lucanidæ—Pseudolucanus capreolus (L.) (Fig. 90)
- 91. Passalidæ—Passalus cornutus Fab. (Fig. 91)

CERAMBYCOIDEA

- 92. Cerambycidæ—Tetraopes tetraophthalmus (Forst.) (Fig. 92)
- 93. Chrysomelidæ—Leptinotarsa decemlineata (Say) (Fig. 93)

94. Mylabridæ-Mylabris discoideus Say (Fig. 94)

BRENTOIDEA

95. Brentidæ—Eupsalis minuta Drury (Fig. 95)

CURCULIONOIDEA

96. Platystomidæ—Platystomus albinus L. (Fig. 97)

97. Belidæ—Ithycerus noveboracensis (Forst.) (Fig. 96)

98. Curculionidæ—Lixus concavus Say (Fig. 98)

Asynonychus godmani Crotch (Fig. 99)

SCOLYTOIDEA

99. Platyopodidæ—Platypus cylindricus Fab. (Fig. 100)

100. Scolytidæ—Dendroctonus valens Lec. (Fig. 101)

GENERAL MORPHOLOGY

For a general discussion of the morphology of the coleopterous labium and maxilla, it is desirable to choose as a basis a generalized form exhibiting primitive characters. The extreme range in variations of the structures concerned makes the selection of a species for general description rather difficult. Many of the forms studied combine generalized and specialized features in a bewildering fashion. Since Crampton (1925) has homologized the labium of *Silpha* with the type exhibited by the primitive and "ancestral" roach, *Periplaneta*, and Forbes (1922) has indicated the primitive nature of the wing of *Silpha*, it is probably justifiable to use this genus as a basis for comparison with the rest of the Coleoptera.

LABIUM: In the labium of Silpha americana (Fig. 13) the gular region (gu) is somewhat narrowed and is not demarked from the submentum (sm). The gular pits (gp), the openings of the invaginations of the posterior tentorial arms, are considered as the anterior limits of the gula. In many Coleoptera these pits are lost with the inrolling of the head capsule and consequent obliteration of the gula, or with the extension of the posterior tentorial arms along the partial or entire length of the gular sutures. The gular sutures (gs) which are distinct and separated in Silpha demark the gula from the rest of the head capsule.

In Silpha, as in most of the other Coleoptera considered, the

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submentum (sm) is not demarked from the gula but is distinct from the mentum (mn). The mentum, on the other hand, is usually a distinctly defined region but is very variable in contour when compared throughout the order. A membranous region, the mental membrane (mem), which lies between the palpigers and mentum, is present in many forms, including Silpha. In some cases the mental membrane is confluent with the mentum, but in Silpha the demarkation is definite.

The palpigers (pgr) bears the labial palpi (lp) distally and, throughout the coleopterous families, exhibit a rather wide variation of arrangement. They may be widely separated by the intervening ligula; they may be moderately separated, as in Silpha; and they may be contiguous or even fused indistinguishably in many instances. In the last case, it is probable that the fusion may involve the labial stipites as well as the palpigers, and since neither can be distinguished, the region of fusion is considered as the prementum.

The labial palpi (lp) are usually present and are three-segmented. There is a great diversity of size and shape of these three segments of the palpus. In some forms, they are so small that the palpus is hardly discernible. *Calviger* (Fig. 19) and *Eupsalis* (Fig. 95) are the only species studied in which the labial palpi are entirely lacking. The terminal segment in most forms has a membranous area at the tip which is undoubtedly sensory.

The ligula (lg) lies between, and distal to, the palpigers. It is formed by the union of the glossæ and paraglossæ which fuse in varying degrees. In *Silpha* the paraglossæ (pgl) are distinguishable as comparatively wide membranous lobes, but the glossæ have been lost in the fusion. The ligula also shows a great range of structure. It is large, broad, and sclerotized in *Laccophilus* (Fig. 5), very small in *Eros* and *Lucidota* (Figs. 24, 25), and lacking in such highly specialized forms as *Asynonychus* and *Platypus* (Figs. 99, 100).

MAXILLA: The maxilla is composed if the cardo, stipes, lacinia, galea, palpifer, and maxillary palpus. All of these structures vary greatly when compared throughout the families. The cardo (ca) is the most proximal segment of the maxilla. In Silpha

(Fig. 13), the cardo is not divided into a basicardo (bc) and disticardo (dc), nor is it so divided in most of the other beetles figured. *Cantharis* (Fig. 27), however, does exhibit this division. One of the commonest modifications of the cardo in Coleoptera is its elongation as illustrated by *Mylabris* (Fig. 94) or *Platystomus* (Fig. 97). The cardo always bears a basal process serving for the attachment of the tendons of the adductor and abductor muscles of the maxilla. The basal process of *Silpha* is not so typical as that of other beetles such, for example, as that of *Clambus* (Fig. 12), in which the tendon of the adductor muscle is attached to the inner lobe of the basal process, and the abductor muscle is attached to the outer lobe of the basal process. The point between these two lobes of the basal process serves as a pivot for articulation against the side of the submentum.

The stipes, in most of the Coleoptera figured, is composed typically of the basistipes (bs) and the mediostipes (ms). A dististipes, which is a small membranous area between the basigalea and basistipes, is present in many forms, but is probably best defined in Cicindela (Fig. 1) and Silpha (Fig. 13). The basistipes in *Silpha* is triangular in shape. Its base is contiguous with the margin of the cardo, its outer margin with the palpifer, and its inner margin with the mediostipes. In the majority of figures, the basistipes is roughly triangular in outline, but it may be broad and irregular, as in *Eros* and *Phengodes* (Figs. 24, 26), or elongate, as in Passalus (Fig. 91). In Trichopteryx (Fig. 18), the basistipes is fused with the palpifer. The mediostipes (ms)is, as a rule, irregular in outline and is variable in size. It is often fused with, or poorly demarked from, the lacina (la) (see Figs. 10, 12, 18, etc.). In the cases where the mediostipes is distinct from the lacinia, the extent of its basal margin corresponds to the area to which the basimaxillary membrane is attached. Thus, in beetles which have the mediostipes and lacinia fused, the attachment of the basimaxillary membrane determines the limit of the basal region of the mediostipes. Tropisternus (Fig. 9) is the only form studied in which the parastipes (ps)occurs. It lies between the mediostipes and the lacinia, being strongly separated from the former by a distinct suture and weakly demarked from the latter.

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The maxilla typically bears two lobes, an inner lobe, the lacinia (la), and an outer lobe, the galea (ga). Some of the species figured have only one lobe which is not differentiated into a lacinia and galea. Following Böving and Craighead (1930), this single maxillary lobe is designated as the "mala" (ma) (see Figs. 8, 63, 73, etc.). Both the galea and lacinia show a remarkable range of modifications when compared throughout the Coleoptera. In many forms, the galea is divided into a basal region, the basigalea (bg) and a distal region, the distigalea (dg). The distigalea, as shown in Silpha, may be tipped with a dense tuft of setæ, while in other beetles it is naked (Figs. 1-8), or has setæ sparsely arranged (Fig. 17). The setæ may also be arranged in rows (Fig. 9) or in a brush (Fig. 100). The lacinia differs greatly in form, and bears setæ and spines in a number of diversified arrangements. The lateral margin of the lacinia is usually covered with setæ or spines and at its apex, as in Silpha, the Caraboidea, and a few other forms, may bear a digitus which in Cicindela (Fig. 1), is a moveable process (dig).

In most of the Coleoptera studied, the maxillary palpus is foursegmented, but in some more specialized forms only three segments are apparent (see Figs. 95, 96, 98, 99, etc.). The basal segment of the palpus articulates with the palpifer (pfr), which is usually distinct, but may be fused with the basistipes.

PHYLOGENETIC ASPECTS

ADEPHAGA

Caraboidea

A comparative study of the labium and maxilla of Coleoptera indicates that the families of the Adephaga, namely the Cicindelidæ, Carabidæ, Amphizoidæ, Omophronidæ, Haliplidæ, Dytiscidæ, and Gyrinidæ, undoubtedly form the closest and best defined group of any in the entire order. Leng (1920), Stickney (1923), and Tanner (1927) place this group as the most primitive in the phylogenetic scheme. From the standpoint of the labium and maxilla alone, however, these families exhibit specialization when compared with a form like Silpha (Fig. 13) which was selected as a representative of the family Silphidæ. Crampton (1925) has homologized the labium of Silpha with that of

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the primitive and "ancestral" roach, *Periplaneta*, on the one hand, and, on the other, with the labium of the carabid, *Harpalus*

A comparison of *Harpalus* (Fig. 2) with Silpha (Fig. 13) indicates that *Harpalus* is specialized in the following features: the ligula is narrowed and crowded forward; the palpigers are elongated; the mentum is enlarged; the submentum is reduced; the gula is very narrow due to the inrolling of the head capsule and consequent invagination of the lateral areas of the gula. The maxilla of *Harpalus* also exhibits the following modifications when compared with that of *Silpha*: the cardo, stipes, and lacinia are narrowed; the membranous dististipes is lost; the galea is a slender process. In view of these facts, the family Silphidæ which is undoubtedly related to the families of the Adephaga, should be considered as more primitive than the Adephagous families.

The family Cicindelidæ, represented by *Cicindela* (Fig. 1), is considered by Leng (1920) to be the most primitive of the Coleoptera. When the figures of the labium and maxilla are compared (Figs.1, 2–7), it is evident that the family Cicindelidæ is more specialized than the rest of the Adephagous families. The ligula is lacking, the submentum is very small, and the maxilla is elongated and has an articulated digitus. Comparison of Figs. 1–7 clearly shows the similarity of structure of both the labium and maxilla throughout the Adephagous series, and it is evident that the family Paussidæ (see Fig. 8), although more highly specialized, should be included in this series.

Gyrinoidea _

The superfamily Gyrinoidea includes one family, the Gyrinidæ, represented by *Dineutes* (Fig. 7). This family is so closely related to the families of the Caraboidea it should be included in this superfamily.

POLYPHAGA

Hydrophiloidea

The superfamily Hydrophiloidea contains only one family, the Hydrophilidæ, represented by *Tropisternus* (Fig. 9). According to Stickney's studies of the head capsule and Tanner's studies of the female genitalia, the Hydrophilidæ should be grouped with

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the Adephaga, since its characters are similar to those of the Dytiscidæ and Gyrinidæ. The comparative study of the labium and maxilla, however, does not warrant the grouping of the Hydrophilidæ with the Adephagous families. The nature of the labium and maxilla of *Tropisternus* (Fig. 9) indicates that the family Hydrophilidæ more closely resembles some of the families of the Polyphaga, the less specialized Silphidæ, for example (see Fig. 13). This grouping of the superfamily Hydrophiloidea with the Polyphaga supports Forbes' studies of the wings and Leng's classification.

Silphoidea

The superfamily Silphoidea, as listed by Leng, includes the families Platypsillidæ, Leptinidæ, Silphidæ, Clambidæ, Scydmænidæ, and Orthoperidæ (Figs. 10–15). Silpha is probably the most generalized of any form figured in this series. Its resemblance to the Caraboids has already been indicated and it is also very similar to Staphylinus (Fig. 16) among the Staphylinoidea. Tanner places the Staphylinidæ in the silphoid series, while Forbes places the two families as very near together forming "an isolated group apparently not nearer the Polyphaga than Adephaga."

Platypsylla, although rather highly specialized, clearly resembles Leptinus in the characters of the labium, particularly in the lobed nature of the mentum. Leptinus resembles Silpha in the structure of both the labium and maxilla. The Scydmænid, Euconnus, and the Orthoperid, Orthoperus, also resemble Silpha. In the superfamily Silphoidea, the labium in characterized by a broad ligula, a comparatively long submental region demarked from the head capsule laterally, and distinct gular sutures and gular pits. The maxilla in all forms has the mediostipes confluent with the lacinia, and the galea divided into a basigalea and distigalea.

Staphylinoidea

The superfamily Staphylinoidea is comprised of eight families, namely, the Staphylinidæ, Pselaphidæ, Clavigeridæ, Ptilidæ, Sphæriidæ, Scaphidiidæ, Sphæritidæ, and Histeridæ (Figs. 16– 23). In this superfamily, the labium and maxilla show a rather diversified structure as indicated in the figures. As mentioned above, *Staphylinus* strongly resembles *Silpha* in having the submentum comparatively long and confluent with the narrow gula, in having gular sutures and pits distinct, and in having the structure of the maxilla essentially similar. The silphoid family Clambidæ, represented by *Clambus* (Fig. 12), resembles the staphylinoid families Ptilidæ, represented by *Trichopteryx* (Fig. 18), and Sphæriidæ, represented by *Sphærius* (Fig. 20). In these three families, the general character of the maxilla is the same. The gular region is short, and the submentum is only weakly demarked from the head capsule. *Scaphidium* and *Hister* are alike in having confluent gular sutures and a reduced submental region. *Pselaphus*, although specialized, bears a striking resemblance to *Euconnus. Claviger*, which is also specialized, can be placed near *Pselaphus*.

Cantharoidea

The superfamily Cantharoidea is a comparatively close knit group which includes the families Lycidæ, Lampyridæ, Phengodidæ, Cantharidæ, Melyridæ, Cleridæ, and Corynetidæ (Figs. 24–30). Within this group, the Lycidæ and Lampyridæ as represented by *Eros* and *Lucidota* are very similar. In both forms the gula is short and broad, the mentum and submentum are small and weakly demarked, the palpigers are fused, and the ligula and labial palpi are essentially alike. The maxillæ are also very similar. The Phengodidæ and Cantharidæ, represented by *Phengodes* and *Cantharis*, can be grouped together. The gula in these two forms is longer than in *Eros* and *Lucidota*.

The clerid, *Trichodes*, and Corynetid, *Charriessa*, are strikingly similar in the structure of the maxilla. Both of the last two genera in the general characters seem to resemble the members of the Mordelloidea more closely than they resemble the members of the Cantharoidea as is indicated by the breadth of the ligula, the demarkation of the mentum, the development of the gula, the division of the maxillary galea into a basigalea and distigalea, and the development of a long, distinct lacinia. The family Melyridæ as represented by *Malachius* resembles the Cleridæ in having a similar structure of the labium. In both

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cases, the ligula is membranous, the palpigers are contiguous, and the mentum is weakly developed and poorly demarked from the mental membrane. In *Malachius*, the submentum is weakly demarked from the gula and the gular pits extend the length of the gula sutures, while in *Trichodes*, the submentum is confluent with the gula and the gular pits extend the length of the gular sutures. The above mentioned affinities of the Cantharoidea are in general agreement with Stickney's views of the group.

Lymexyloidea

Unfortunately, a single family of the Lymexyloidea must be relied upon in attempting to determine the affinities of this group, because representatives of the other two families, the Teleguesidæ and Micromalthidæ, were unobtainable. The Lymexylidæ are represented in this discussion by Hylcoetus. Although rather specialized, this genus seems to resemble the Dryopoid genus *Psephenus* (Fig. 51), particularly in the structure of the maxilla. In both genera, the stipes is not differentiated into a basistipes and mediostipes and is confluent with the lacinia, and the palpifer is a ring-like segment. In the labium in both forms, the palpigers are contiguous, or nearly so, and the submentum is weakly demarked from the head capsule and is confluent with the wide gula. Stickney and Tanner both place this superfamily with the Cucujoidea.

Cupedoidea

The Cupedoidea contains one family, the Cupedidæ, represented by *Cupes* (Fig. 33). Although the form studied is somewhat specialized, the labium resembles this structure in some of the families of the Mordelloidea. The palpigers are widely separated, the mentum is large, the submentum is weakly demarked from the head capsule and is confluent with the gula as is the case in representatives of the Cephaloidæ and Mordellidæ (Figs. 34, 35). Apparently the superfamily Cupedoidea should be grouped with the superfamily Mordelloidea as Stickney and Tanner have indicated.

Mordelloidea

Representatives of eleven of the twelve families listed under the superfamily Mordelloidea have been figured (see Figs. 31, 34-43), and the group, as a whole, shows considerable homogeneity of structure in the labium and maxilla. In the labium in most of these forms, the ligula is broad and bilobed, the mentum is well developed, the submentum is confluent with the long gula and is demarked from the head capsule, and the gular pits are usually distinct. In the maxilla, the mediostipes is, in most cases, demarked from the lacinia, and the galea in divided into a basigalea and distigalea. The Rhipiphoridæ and the Meloidæ, represented by *Rhipiphorus* and *Nemognatha*, show a striking similarity in the great elongation of the distigalea of the maxilla and the close association of the lacinia with the basigalea.

As Stickney has pointed out, the Oedemeridæ, Cephaloidæ, Pyrochroidæ, Pedilidæ, and Anthicidæ are closely related. All of these forms (see Figs. 34, 35, 40, 41, 42) have the ligula broad and bilobed, the mentum distinct, and the submentum confluent with the long gular region. In all but *Notoxus*, which represents the Anthicidæ, the mediostipes of the maxilla is demarked from the lacinia. The general nature of the labium and maxilla of *Othnius*, *Tomoxia*, and *Pytho* would seem to group the families Othniidæ, Mordellidæ, and Pythidæ within this series.

Elateroidea

The superfamily Elateroidea, as listed by Leng, includes the families Cerophytidæ, Cebrionidæ, Plastoceridæ, Rhipiceridæ, Elateridæ, Melasidæ, Throscidæ, and Buprestidæ (Figs. 44–50). A representative of all of these families has been figured except for the Plastoceridæ. The Cerophytidæ, represented by *Cerophytum*, the Melasidæ, represented by *Eucnemis*, and the Throscidæ, represented by *Throscus*, seem to be related. In these three forms, the submentum and gula are broad and greatly shortened, the mentum is well developed, the palpigers are contiguous, or nearly so, and the maxillary galea and lacinia are short and comparatively broad.

The representatives of the Elateridæ and Buprestidæ, Alaus and Buprestis, are similar, particularly in the structure of the maxilla. The mediostipes is demarked from the lacinia, and the lacinia is comparatively short and is membranous in its basal region. In the labium, the mentum is broad and bears a weak, transverse, median division, the gula is broad, and the gular pits

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are distinct. The Cebrionidæ, represented by *Cebrio*, resembles the Elaterid, *Alaus*. The ligula is bilobed, the mentum is weakly divided transversely, and the maxillary mediostipes is demarked from the short lacinia. The family Rhipiceridæ, represented by *Sandalus*, is probably related to the Cantharoids. The general nature of the labium and maxilla seem to ally it with the characters found in this group.

Dryopoidea

The superfamily Dryopoidea is composed of the families Psephinidæ, Dryopidæ, Helmidæ, Heteroceridæ, and Georyssidæ (Figs. 51-55). With the exception of *Georyssus* and *Psephenus*, this group seems to be related to the Elateroidea. *Georyssus* seems to resemble *Hister*. Comparison of Figs. 54 and 23 shows a similarity in the structure of the labium and maxilla. The ligula is bilobed; the mentum is distinct; the submentum is tapered posteriorly; the gular region, which has been obliterated by the inrolling of the head eapsule, is represented by a median suture; the mediostipes of the maxilla is demarked from the lacinia; the lacinia is slender; and the palpifer is large.

The shortened submental and gular regions in the Heteroceridæ, represented by *Heterocerus*, would suggest its relation to the Cerophytidæ, Melasidæ, and Thoroscidæ. *Potamophilus*, representing the Dryopidæ, and *Helmis*, representing the Helmidæ, are similar. The palpigers are contiguous; the mentum is distinct; the submentum is weakly demarked from the narrow gula; the lacinia of the maxilla is comparatively long; the galea is divided into a basigalea and distigalea; and the mediostipes is weakly demarked from the lacinia in *Potamophilus*, and is confluent with the lacinia in *Helmis*.

Dascilloidea

The superfamily Dascilloidea includes two families, the Dascillidæ and Helodidæ (Figs. 56, 57). The similarities in the characters of the labium show that these two families are probably closely related. The mentum is wide and distinctly demarked, the submentum is demarked from the head capsule, and is confluent with the wide gula. In the maxilla of the Helodid, *Scirtes*, the mediostipes is demarked from the lacinia, while in *Dascillus* it is confluent with the lacinia.

Byrrhoidea

In the superfamily Byrrhiodea, representatives of the Chelonariidæ, Dermestidæ, and Byrrhidæ have been figured (Figs 58– 60). Stickney includes the Chelonariidæ in the Dascilloidea. Comparison of Fig. 58 with Fig. 56 shows that, although *Chelonarium* is somewhat more specialized than *Dascillus*, the two genera are undoubtedly closely related and therefore the Chelonariidæ are perhaps more appropriately grouped with the Dascilloidea than with the Byrrhiodea. *Dermestes* and *Byrrhus* (Figs. 59, 60) are apparently closely related to the Cucujoidea and are therefore discussed with this group.

Rhysodoidea

The superfamily Rhysodoidea contains one family, the Rhysodidæ, represented by *Rhysodes* (Fig. 61). This form is so specialized that it is difficult to place it with any degree of certainty. The development of the mentum and the narrowing of the gula suggest a relationship to the Cucujoidea in general, and to Cucujus in particular.

Cucujoidea

The superfamily Cucujoidea, according to Leng, includes more families than any other superfamily. Representatives of seventeen of the eighteen families have been figured, a representative of the Monoeidæ being unobtainable (Figs. 62–77). The Nitidulidæ and Lathridiidæ, represented by *Prometobia* and *Lathridius* (Figs. 63, 73), are alike in having the mentum very broad, the submentum broad and not demarked from the head capsule, and only a single maxillary lobe, the mala, present.

The Rhizophagidæ, Derodontidæ, Cryptophagidæ, Colydiidæ, and Dermestidæ (see Figs. 64, 68, 69, 71, 59) are alike in having the mentum well developed, the submentum confluent with the gula and demarked from the head capsule, the gula broad, and the gular pits distinct. The maxilla has the mediostipes confluent with, or weakly demarked from, the lacinia, except in *Dermestes* which has the demarkation distinct. In all of these forms, the lacinia and galea are comparatively long and slender, and, in all except *Rhizophagus*, the galea is divided into a basigalea and distigalea, and the lacinia terminates in a claw-like process. Sept., 1938]

The Erotylidæ, Murmidiidæ, Mycetaeidæ, Endomychidæ, and Phalacridæ (Figs. 67, 72, 74, 75, 76) are similar in having the mentum well developed; the submentum short and demarked from the encroaching head capsule, which widely separates the distinct region of the submentum from the gula; and the gula extremely short and demarked by distinct gular pits. The maxilla in this group, with the exception of the Mycetaeidæ, has the galea divided into a basigalea and distigalea; the lacina long and slender; and the mediostipes demarked from the lacina, except in the Erotylidæ. The family Monotommidæ, represented by *Monotoma* (Fig. 65), probably belongs in this group, although the gula is somewhat longer in this form, and the gular pits extend the length of the gular sutures.

The Ostomidæ, Cucujidæ, and Mycetophagidæ (Figs. 62, 66, 70) have the anterior region of the submentum wide and demarked from the head capsule, and the posterior region narrowed and confluent with the gula. The gular pits are distinct in *Mycetophagus*, but extend the length of the gular sutures in *Ostoma* and *Cucujus*.

Byrrhus (Fig. 60) does not resemble any genus figured for the Cucujoidea in all respects, but is similar to the more specialized Ostoma (Fig. 62) in the characters of the labium and maxilla. The Coccinellidæ, represented by Leptinotarsa (Fig. 77), might be placed either with the Cucujoidea, or with the Tenebrionoidea.

Several families of the Cucujoidea strongly resemble families of the Mordelloidea, showing that these two groups are, without doubt, closely related. *Cucujus* (Fig. 66) is very similar to *Pytho* (Fig. 39) in the characters of the labium and maxilla. The Mordelloids *Tomoxia*, *Pedilus*, *Pyrochroa*, *Notoxus*, etc. (Figs. 35, 40, 41, 42, etc.) resemble such Cucujoids as *Rhizophagus* and *Derodontus* (Figs. 64, 68) in their general characters.

Tenebrionoidea

The superfamily Tenebrionoidea includes the Alleculidæ, Tenebrionidæ, Lagriidæ, Monommidæ, and Melandryidæ (Figs. 78-82). These families form a comparatively homogenous group. In all of these families excepting the Monommidæ, represented by *Monomma* (Fig. 81), the labium has the anterior region of the submentum broad, and at least weakly demarked from the encroaching capsule, and the posterior region either obliterated or represented by a median suture, as in *Arthromacra* (Fig. 80), or by a Y-shaped suture, as in *Alobates* and *Penthe* (Figs. 79, 82). The gular pits extend along the gular sutures in *Arthromacra*, but are distinct in the other genera. The maxillae are similar in all the forms figured in this group. The mediostipes is demarked from the lacinia and the galea is divided into a basigalea and distigalea. The Tenebrionoidea as a whole seem closely related to the Mordelloidea and Cucujoidea.

Bostrichoidea

The superfamily Bosterichoidea is comprised of the Ptinidæ, Anobiidæ, Bostrichidæ, Lyctidæ, Sphindidæ, and Cisidæ (Figs. 83-88). The Ptinidæ and Sphindidæ (Figs. 83, 87) are similar in having the ligula bilobed and sclerotized, the submentum weakly demarked from the head capsule, the gular pits extending along the gular sutures, the mediostipes confluent with the lacinia, and the galea not divided into a basigalea and distigalea.

The Anobiidæ, Bostrichidæ, and Lyctidæ (Figs. 84, 85, 86) have a trilobed ligula, distinct gular pits, a comparatively slender gula, the maxillary mediostripes confluent with, or weakly demarked from, the lacinia, and the galea divided into a basigalea and distigalea. The family Cisidæ represented by *Cis* (Fig. 88) is rather specialized in the loss of the ligula, the narrowing of the labium, and the shortening of the galea and lacinia. Except for the loss of the ligula, the labium resembles that of the Mordelloid family Rhipiphoridæ (Fig. 37).

Scarabaeoidea

The superfamily Scarabaeoidea includes the Scarabæidæ, Lucanidæ, and Passalidæ, represented by *Geotrupes, Pseudolucanus*, and *Passalus* (Figs. 89, 90, 91). This group is homogeneous, and is undoubtedly related to the families of the Adephaga and their close relatives. The mentum is very broad, the submentum is broad and weakly demarked from the wide gula, the gular pits extend along the gular sultures, and the maxillary mediostipes is confluent with, or only weakly demarked from, the lacinia. *Passalus* (Fig. 91) resembles *Amphizoa* (Fig. 6), particularly in the character of the maxilla, and apparently is more specialized SEPT., 1938]

than Geotrupes and Pseudolucanus. Geotrupes appears to be the least specialized of this series. In this form, the mentum and submentum are not so broad, the ligula is sclerotized and bilobed, and the palpigers are widely separated. Pseudolucanus would seem to occupy an intermediate position between Geotrupes and Passalus. The mentum and submentum are wide. The ligula is bilobed and sclerotized, and the palpigers are narrowly separated. In Passalus the mentum and submentum are wide, the ligula is broad and sclerotized, and the palpigers are fused in the premental region.

Cerambycoidea

The superfamily Cerambycoidea is composed of three families, the Cerambycidæ, Chrysomelidæ, and Mylabridæ (Figs. 92, 93, 94). These families form a homogeneous group in which the ligula is broad and sclerotized, or partly so, the palpigers are fused in the premental region, a mental membrane is present, the mentum is short, and the maxillary mediostipes is confluent with the lacinia or weakly demarked from it. In *Tetraopes* (Fig. 92), the submentum is confluent with the wide gula, and the gular pits extend along the gular sutures. Except for the demarkation of the anterior region of the submentum, *Leptinotarsa* resembles *Tetraopes* in the nature of the submentum and gula. *Mylabris* has the anterior region of the submentum enlarged and cut off from the narrowed gula by the encroaching head capsule.

Brentoidea

The superfamily Brentoidea has one family, the *Brentida*, represented by *Eupsalis* (Fig. 95). This genus is highly specialized and should be included in the superfamily Curculionoidea, to which it is closely related. The labium lacks the labial palpi and palpigers; the mentum is confluent with the elongated submentum; the gula has been obliterated, and is represented by a median gular suture; the maxillary cardo and stipes are fused to form a narrow strip; there is a single maxillary lobe; and the maxillary palpus is three-segmented.

Curculionoidea

The superfamily Curculionoidea includes the Platystomidæ, Belidæ, and Curculionidæ. The family Platystomidæ, represented

by *Platystomus* (Fig. 97), although highly specialized, suggests the Adephaga in the breadth of the labium and general nature of the maxilla, found in the Adephagous family Cicindelidæ. The family Belidæ, represented by *Ithycerus* (Fig. 96), resembles the more specialized Scolytidæ, represented by Dendroctonus (Fig. 101). The ligula in both of these forms is short; the palpigers are lacking; the mentum is wide in Ithycerus, but narrow in Dendroctonus; the submentum is long and wide in Ihycerus, but short and confluent with the head capsule laterally in *Dendroc*tonus; and, in both, the gula is represented by a median suture. The maxilla in *Dendroctonus* is more highly specialized in having the basistipes, mediostipes, and palpifer fused and in having a single maxillary lobe, the mala, present. In Ithycerus, however, the basistipes, mediostipes, palpifer, galea, and lacinia are all distinctly demarked. In both of these genera, the maxillary palpus is three-segmented.

The family Curculiondæ is represented by *Lixus*, a form with a long snout (Fig. 98), and *Asynonychus*, a form with a short snout (Fig. 99). Both of these genera are specialized. *Lixus* has minute labial palpi, a comparatively broad ligula, a greatly elongated submental region, and the gula represented by a median suture. In the maxilla, the stipes is not differentiated into a basistipes and mediostipes, and is confluent with the mala. *Asynonychus* has the labial palpi larger, but lacks the ligula, and the submental region is short. The maxilla has the stipes weakly differentiated into a basistipes and mediostipes, and the galea and lacinia are both present. In both of these genera, the maxillary palpus is three-segmented.

Scolytoidea

The superfamily Scolytoidea includes two families, the Scolytidæ (Fig. 101) discussed above, and the Platypodidæ, represented by *Platypus* (Fig. 100). *Platypus* is also specialized, especially in the features of the maxilla. The labium is similar to that of *Asynonychus*, but the maxilla appears to resemble that of *Eupsalis*.

In summarizing the affinites of the superfamilies of the Coleoptera as indicated by the comparative study of the labium and maxilla, two principal groups are recognizable which agree with Sept., 1938]

Stickney's grouping of the superfamilies based on the study of the head capsule. The first of these groups includes the following superfamilies: Caraboidea, Gyrinoidea, Hydrophiloidea, Silphoidea, Stanphylinoidea, Cantharoidea (in part), and Scarabaeoidea.

The second and larger group includes the following superfamilies: Cantharoidea (in part), Lymexyloidea, Mordelloidea, Elateroidea, Dryopoidea, Dascilloidea, Byrrhoidea, Rhysodoidea, Cucujoidea, Tenebrionoidea, and Bostrichoidea.

The superfamilies Cerambycoidea, Brentoidea, Curculionoidea, and Scolytoidea might be grouped separately. Due to the specializations occurring in them, it is extremely difficult to determine to which of these two main groups they are most closely related.

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Plate XIII

Figure 1. Cicindelidæ—Cicindela sexquttata Fab. Figure 2. Carabidæ—Harpalus caliginosus (Fab.) Figure 3. Omophronidæ-Omophron americanum Dej. 4. Haliplidæ—Laccophilus maculosus (Germ.) Figure Figure 5. Dytiscidæ-Colymbetes sculptilis Harr. Figure 6. Amphizoidæ—Amphizoa isolens Lec. 7. Gyrinidæ—Dineutes vittatus (Germ.) Figure 8. Paussidæ-Paussus hova Figure 9. Hydrophilidæ—Tropisternus glaber (Hbst.) Figure

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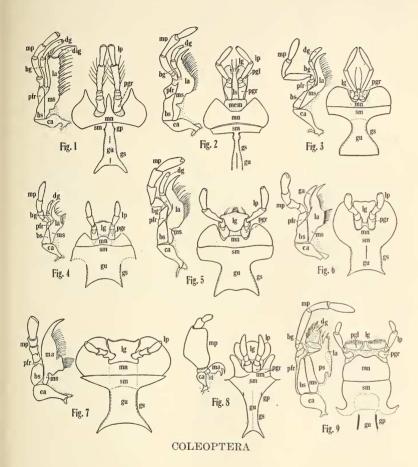


PLATE XIV

Figure 10. Platypsyllidæ—Platypsyllus castoris Rits.

Figure 11. Leptinidæ—Leptinus testaceus Müll.

Figure 12. Clambidæ-Clambus punctulatum Beck.

Figure 13. Silphidæ-Silpha americana L.

Figure 14. Scydmænidæ-Euconnus similis Blatch.

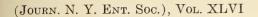
Figure 15. Orthoperidæ-Orthoperus brunnipes Gyll.

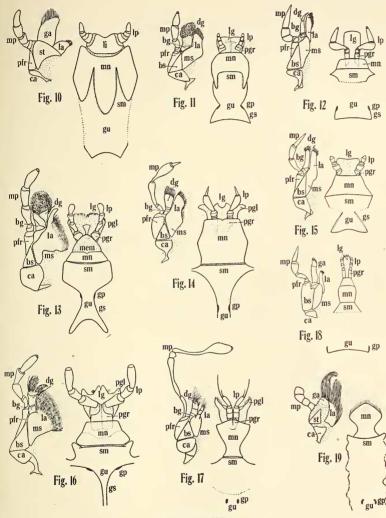
Figure 16. Staphylinidæ-Staphylinus vulpinus Nordm.

Figure 17. Pselaphidæ-Pselaphus dresdensis Herbst.

Figure 18. Ptilidæ-Trichopteryx lata Motsch.

Figure 19. Clavigeridæ-Clavigera testaceus





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PLATE XV

Figure 20. Sphæriidæ-Sphærius acaroides Waltl.

- Figure 21. Scaphidiidæ-Scaphidium quadrimaculatum Oliv.
- Figure 22. Sphæritidæ—Sphærites glabratus (Fab.)

Figure 23. Histeridæ-Hister obtusatus Harris

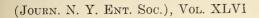
Lycidæ—Eros aurora Hbst. Figure 24.

Figure 25. Lampyridæ—Lucidota atra (Fab.)

Figure 26. Phengodidæ-Phengodes sp.

Figure 27. Cantharidæ-Cantharis andersoni Frost.

Figure 28. Melyridæ-Malachius æneus (L.)



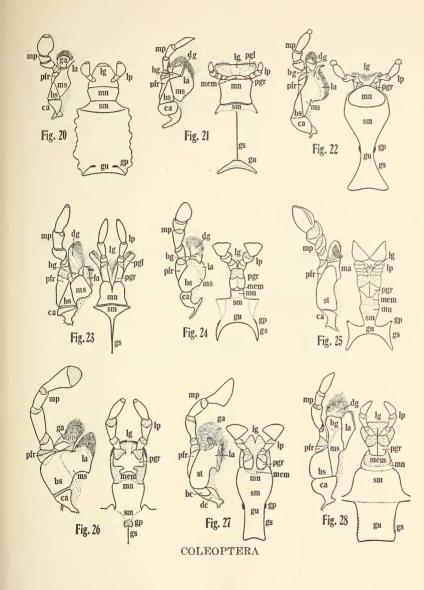


PLATE XVI

Figure 29. Cleridæ—Trichodes ornatus Say

Figure 30. Corynetidæ-Chariessa pilosa Forst.

Figure 31. Othniidæ-Othnius kraatzi

Figure 32. Lymexylidæ-Hylocætus dermestoides L.

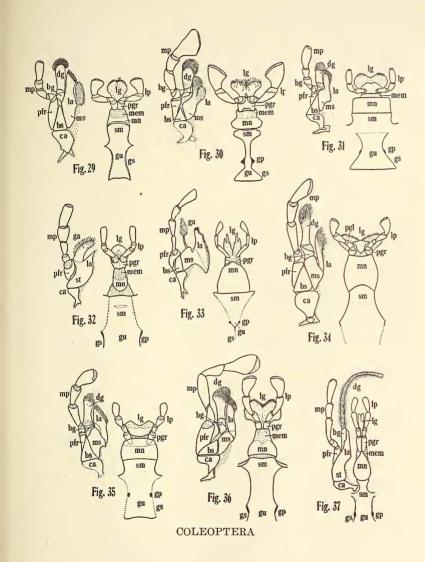
Figure 33. Cupesidæ-Cupes latrellei Sol.

Figure 34. Cephaloidæ-Cephaloon lepturides Newm.

Figure 35. Œdemeridæ-Ditylus lævis Fabr.

Figure 36. Mordellidæ—Tomoxia bidentata (Say)

Figure 37. Rhipiphoridæ-Rhipiphorus dimidiatus Fabr.



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Figure 38. Meloidæ—Nemognatha piezata Fab.

Figure 39. Pythidæ-Pytho americanus Kby.

Figure 40. Pyrochroidæ—Pyrochroa coccinea L.

Figure 41. Pedilidæ—Pedilus collaris (Say)

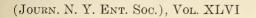
Figure 42. Anthicidæ-Notoxus calcaratus Horn

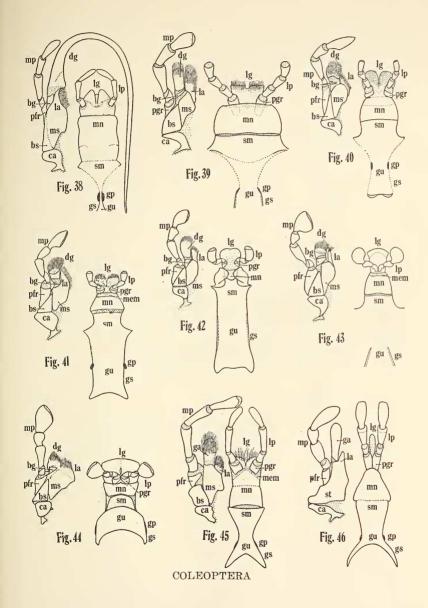
Figure 43. Euglenidæ-Euglenes pruinosus

Figure 44. Cerophytidæ-Cerophytum elateroides Latr.

Figure 45. Cebrionidæ—Cebrio gigas Fabr.

Figure 46. Rhipiceridæ—Sandalus segnis





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Figure 47. Elateridæ—Alaus oculatus (L).

Figure 48. Melasidæ—Eucnemis capucina Ahrens.

Figure 49. Throscidæ-Throscus dermestoides L.

Figure 50. Buprestidæ—Buprestis fasciata Fab.

Figure 51. Psephenidæ—Psephenus lecontei (Lec.)

Figure 52. Dryopidæ-Potamophilus acuminatus Fabr.

Figure 53. Helmidæ-Helmis mangei

Figure 54. Georyssidæ-Georyssus lævicollis Germ.

Figure 55. Heterocidæ-Heterocerus parallelus Krynick

(Plate XVIII)

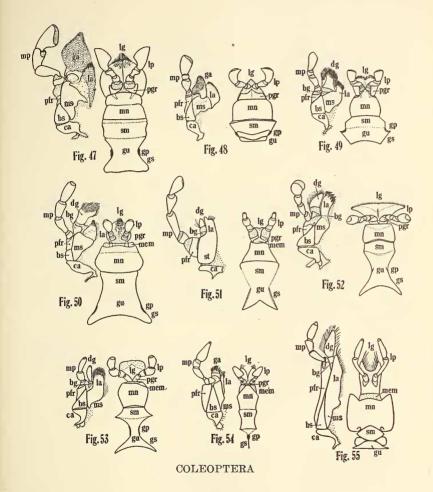


PLATE XIX

Figure 56.	Dascillidæ-	-Dascillus	cervinus	L.
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Figure 57. Helodidæ-Scirtes tibialis Guer.

Figure 58. Chelonariidæ—Chelonarium ornatum Klug

Figure 59. Dermestidæ—Dermestes lardarius L.

Figure 60. Byrrhidæ-Byrrhus americanus Lec.

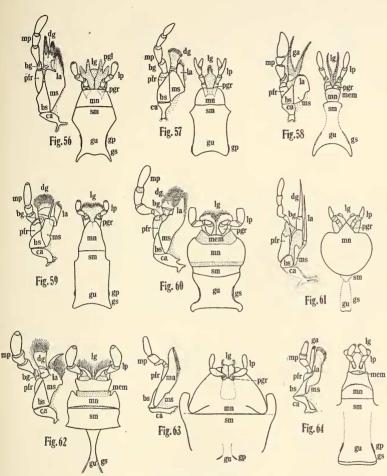
Figure 61. Rhysodidæ-Rhysodes sulcatus Fabr.

Figure 62. Ostomidæ—Ostoma grossa (L.)

Figure 63. Nitidulidæ—Prometobia sexmaculata (Say)

Figure 64. Rhizophagidæ-Rhizophagus picipes Walker

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PLATE XX

Figure 65. Montomidæ-Monotoma conicicollis

Figure 66. Cucujidæ-Cucujus clavipes Fab.

Figure 67. Erotylidæ-Megalodacne grandipennis

Figure 68. Derodontide-Derodontus maculatus Melsh.

Figure 69. Cryptophagidæ-Antherophagus ochraceus Melsh.

Figure 70. Mycetophagidæ—Mycetophagus punctatus Say

Figure 71. Colydiidæ—Trachypholis ornatus

Figure 72. Murmidiidæ-Murmidius ovalis Beck.

Figure 73. Lathridiidæ-Lathridius lardarius De G.

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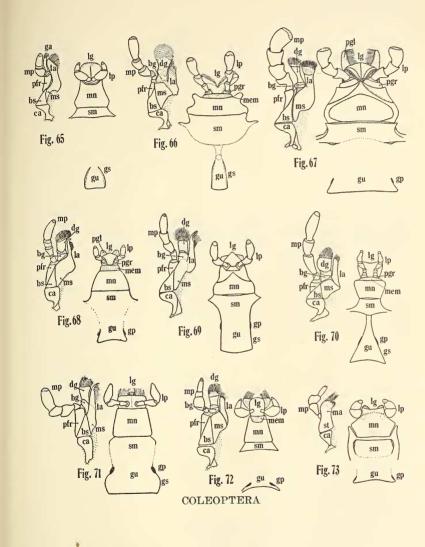
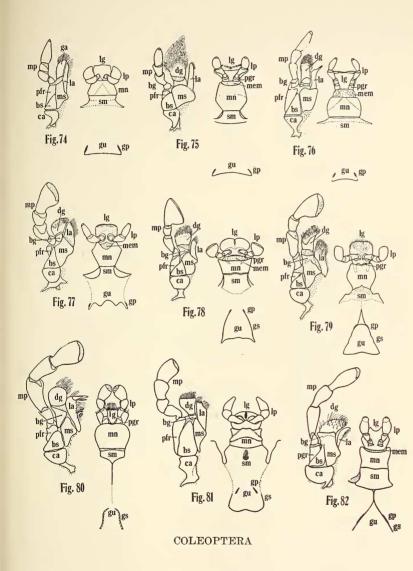


PLATE XXI

Figure	74.	Mycetæidæ—Mycetæa hirta (Marsh.)
Figure	75.	Endomychidæ—Lycoperdina ferruginea Lec.
Figure	76.	Phalachridæ—Phalacrus grossus Erichs.
Figure	77.	Coccinellidæ-Anatis quindecimpunctata (Oliv.)
Figure	78.	Alleculidæ—Hymenorus melsheimeri Csy.
Figure	79.	Lagriidæ—Arthromacra ænea (Say)
Figure	80.	Tenebrionidæ-Alobates pennsylvanica (De G.)
Figure	81.	Monommidæ—Monomma maximum
Figure	82.	Melandryidæ—Penthe obliquata (Fab.)

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Figure 83. Ptinidæ—Oligomerus brunneus Oliv.Figure 84. Anobiidæ—Sitodrepa panicea (L.)Figure 85. Bostrichidæ—Apate terebrans Pall.Figure 86. Lyctidæ—Lyctus linearis (Goeze)Figure 87. Sphindidæ—Sphindus dubius Gyllh.Figure 88. Cisidæ—Cis boleti ScopoliFigure 89. Scarabæidæ—Geotrupes splendidus (Fab.)Figure 90. Lucanidæ—Pseudolucanus capreolus (L.)Figure 91. Passalidæ—Casalus cornutus Fab.

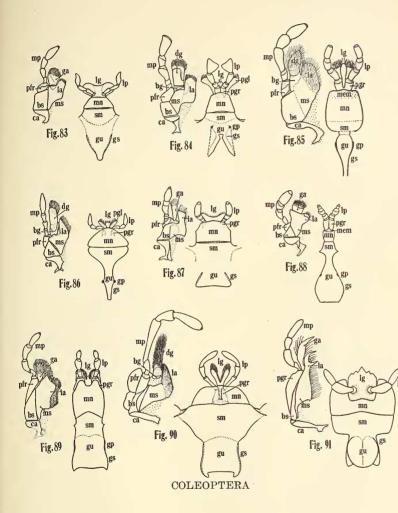


PLATE XXIII

Figure92.Cerambycidæ—Tetraopes tetraophthalmus (Forst.)Figure93.Chrysomelidæ—Leptinotarsa decemlineata (Say)Figure94.Mylabridæ—Mylabris discoideus SayFigure95.Brentidæ—Eupsalis minuta DruryFigure96.Belidæ—Ithycerus noveboracensis (Forst.)Figure97.Platystomidæ—Platystomus albinus L.Figure98.Curculionidæ—Lixus concavus SayFigure99.Curculionidæ—Asynonychus godmani CrotchFigure100.Platypodidæ—Platypus cylindricus Fabr.

Figure 101. Scolytidæ—Dendroctonus valens Lec.

ABBREVIATIONS

bc—basicardo	li—labium	
bg—basigalea	lp—labial palp	
bs—basistipes	ls—labial stipes	
ca-cardo	ma—mala	
dc—disticardo	mem-mental membrane	
dg—distigalea	mn-mentum	
dig-digitus	mp—maxillary palpus	
ga—galea	ms-mediostipes	
gl—glossa	pfr—palpifer	
gp—gular pit	pgl-paraglossa	
gs—gular suture	pgr—palpiger	
gu—gula	ps—parastipes	
la—lacinia	sm—submentum	
lg—ligula	st—stipes	

